

Cross-Sectional Geometric Properties of the *Otavipithecus* Mandible

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ABSTRACT Cross-sectional geometric properties of the postcanine mandibular corpus are determined for the only known specimen of *Otavipithecus namibiensis*, a middle Miocene hominoid from southern Africa. It is shown that *Otavipithecus* is unique in that several important mechanical properties of its mandible, including maximum and minimum moments of inertia and distribution of cortical bone, differ from patterns seen in both extant hominoids and the early hominids *Australopithecus africanus* and *Australopithecus (Paranthropus) robustus*. This is particularly apparent in the mechanical design of the posterior portion of the mandibular corpus for resisting increased torsional and transverse bending moments. Cortical index values at the level of M_2 also reveal that both *Otavipithecus* and *A. africanus* are similarly designed to resist increased masticatory loads with relatively less cortical bone area, a highly efficient mechanical design. © 1996 Wiley-Liss, Inc.

Shape variables, particularly those designed to measure aspects of mandibular robustness, have often been used to characterize the functional morphology of mandibular form in early hominids (e.g., Dart, 1948; Wolpoff, 1975, 1977; White, 1977; Hylander, 1979a, 1988; Chamberlain and Wood, 1985). The prevailing notion is that the thick, robust mandibular corpus of early hominids is an adaptation to resist the high stresses incurred during mastication. Many of these explanations were generated from analyses of the external dimensions of the mandible, without consideration of the distribution of trabecular or cortical bone.

Opinions vary about the “correct” way to analyze mandibular biomechanics. For example, Smith (1983:325) maintained that variables with presumed mechanical implications, such as moments of inertia, “provide no insights beyond those obtained from the analysis of corpus height, breadth, and the ratio between them.” On the other hand, Daegling (1989) has argued that the traditional “robusticity” index is a shape indicator

only and is functionally irrelevant. Since forces generated during mastication, i.e., bending, torsion, etc., increase in any direction with distance from the neutral axis, the ability of the mandible to resist such stresses can be radically altered by changes in the distribution of cortical bone throughout the cross section. Since mandibles are not solid beams, it follows that more refined biomechanical analyses should incorporate information on the cross-sectional distribution of cortical bone (Smith, 1983; Hylander, 1988; Daegling, 1989; Daegling and Grine, 1991). The amount and disposition of cortical bone are useful variables for quantifying the rigidity of a cross section to a variety of mechanical loads. These measurements can sometimes be obtained from physical cross sections, natural breaks, standard radiogra-

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phy, or by computed tomography (CT) (e.g., Biknevicius and Ruff, 1992; Runestad et al., 1993; Jungers and Minns, 1979; Ruff and Hayes, 1983). Computed tomography provides a unique opportunity to safely investigate the internal architecture of mandibular corpora in any plane of interest and to thereby quantify the resistance of any mandibular cross section to mechanical loading.

In spite of the fact that various functional explanations have been advanced to explain the apparent robustness of some Miocene hominoid mandibles (e.g., Andrews, 1971; de-Bonis and Melentis, 1980; Pilbeam, 1982; Alcock, 1984; Andrews and Martin, 1991), very little is actually known about their cross-sectional geometry. This is due, in part, to the inaccessibility of CT scanning facilities at suitable locations and to the destructive nature of physically sectioning precious fossil material. CT techniques have recently been successfully employed to study cross-sectional geometry in mandibles of early hominids and extant hominoids (Daegling, 1989; Daegling and Grine, 1991). Those results demonstrated distinct differences between early hominids and extant hominoids in the internal organization of the corpus and, more importantly for this study, provide a data set which serves as a comparative framework for interpreting the cross-sectional geometry of the *Otavipithecus* mandible.

MATERIALS AND METHODS

For comparative purposes, cross-sectional geometric properties of extant hominoids and fossil hominids were obtained from Daegling and Grine (1991). Their hominoid sample consisted of mandibular specimens belonging to males and females of *Pan*, *Gorilla*, *Pongo*, and *Homo* while their fossil hominid sample consisted of specimens attributed to *Australopithecus africanus* and *Australopithecus (Paranthropus) robustus*. In order to make direct comparisons with their data, coronal CT scans of the *Otavipithecus* specimen (BER I, 191) were taken at the level of both M_1 and M_2 . All CT scans were taken on a Philips CT scanner at the Johannesburg General Hospital with the following scan parameters: slice thickness = 1.5 mm; kv = 120; ma = 200; picture matrix = 512×512 (Fig. 1).

Hard copy CT images were digitized using

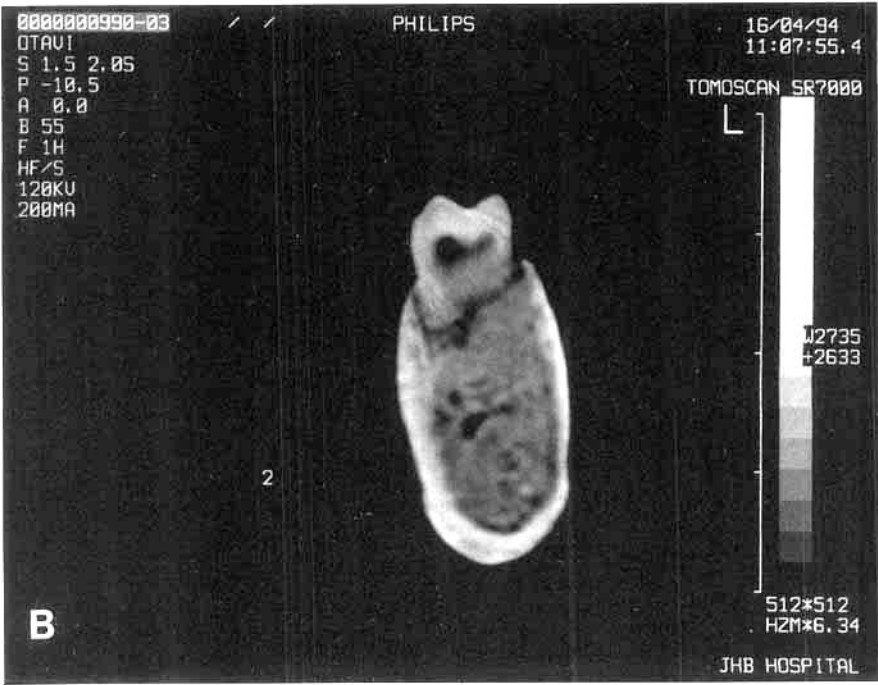
a flatbed Howtek Scanmaster and downloaded into the image analysis program, NIH Image, on a Macintosh fx workstation. It is well-recognized that the window settings (center and width) can affect linear, areal, and volumetric measurements from CT scans (e.g., Ruff and Leo, 1986; Grine, 1991). Because of this, our estimates of the geometric properties for the *Otavipithecus* jaw are based on a range of window settings, the accuracy of which were checked against known linear distances on the *Otavipithecus* mandible. Measurements were calculated from four different images at both the M_1 and M_2 regions of the corpus with each image set to a slightly different window setting. Each variable (i.e., maximum and minimum second moments of area, cortical bone area, total subperiosteal bone area) was calculated three times for each image. From these data, a mean value for each variable was constructed for all four images at M_1 and M_2 . At both the M_1 and M_2 levels, a grand mean, standard deviation, range, and coefficient of variation were calculated for each variable. These values are used for comparisons with the hominoid and hominid data and are reported in Table 1.

Following Daegling (1989), measurements of compact bone area (CBA) and total subperiosteal area (TSA) were calculated for the *Otavipithecus* specimen from the digitized CT images. These two measures were used to calculate a cortical index ($CBA/TSA \times 1,000$) which provides a measure of the relative amount of compact bone within a cross section. The cortical bone component of each cross section was then transferred to another image program, Slice analyzer, which is designed to calculate maximum and minimum second moments of area (I_{max} and I_{min} , respectively).¹ Second moments of area,

¹Aspects of mandibular biomechanics can be determined about either morphological (I_{xx} and I_{yy}) or principal axes (I_{min} and I_{max}). In general, second moments of area around morphological axes are more relevant for consideration of bending rigidity because bending moments produced during mastication occur about morphological axes (Weijjs, 1980). In the posterior corpus of hominoids and early hominids, however, morphological and principal axes are nearly coincident so that corpus (or biomechanical) shape, independent of corpus (or biomechanical) orientation, is a reliable indicator of relative bending rigidity (Daegling, 1990). In the more rostral sections of hominoid corpora (i.e., I_1-P_3), morphological and principal axes diverge markedly due to the inclination of the symphysis.



M₁



M₂

Fig. 1. CT cross section (thickness = 1.5 mm) of the *Otavipithecus* mandible at the level of M₁ and M₂.

TABLE 1. Cross-sectional properties of the *Otavipithecus* mandible at various window settings

Region	Image	Window setting	I_{\min} (mm ⁴)	I_{\max} (mm ⁴)	CBA (mm ²)	TSA (mm ²)
M ₁	1	W2542	1878.3	6802.7	106.4	283.9
		+2333				
	2	W2898	1748.4	5951.4	98.7	280.5
		+2301				
	3	W2955	1740.9	6284.6	104.0	291.9
		+2523				
	4	W3073	1732.9	6015.9	99.6	279.2
		+2464				
	Grand mean		1775.1	6263.7	102.2	283.9
	SD		69.1	387.3	3.6	5.7
M ₂	Range		1732.9–1878.3	5951.4–6802.7	98.7–106.4	279.2–291.9
	CV		3.9	6.2	3.6	2.0
	1	W2210	2051.4	4070.6	86.5	298.7
		+2384				
	2	W2579	2068.6	4220.5	90.9	299.8
		+2278				
	3	W2955	1905.2	3632.1	88.9	300.2
		+2388				
	4	W2955	2173.3	4174.2	89.5	290.6
		+2523				
	Grand mean		2049.6	4024.4	88.9	297.3
	SD		110.3	268.9	1.8	4.5
	Range		1905.2–2173.3	3632.1–4220.6	86.5–90.9	290.6–300.2
	CV		5.4	6.7	2.1	1.5

W, window width; +, window center.

or moments of inertia, take into account not only the amount of cortical bone area, but also the disposition of the cortical bone with respect to a neutral axis (Frankel and Burstein, 1970). It is a measure of the resistance of the cross section to bending in both the parasagittal (I_{\max}) and transverse (I_{\min}) planes.

From the two moments of area, a bending index ($I_{\min}/I_{\max} \times 1,000$) was calculated. This ratio provides a comparative index to assess the relative ability of a cross section to resist twisting, or torsional, stresses (Daegling and Grine, 1991). A low index indicates a decreased ability for a corpus to resist torsional stresses, but at the same time may indicate an increased ability to resist bending in the parasagittal plane as I_{\max} increases in relative magnitude. A high index, on the other hand, indicates increased torsional rigidity as I_{\min} approaches I_{\max} in magnitude, thereby resulting in a more equitable arrangement of cortical bone around the neutral axis. Such an arrangement could also indicate a decreased ability to resist bending in the parasagittal plane through a reduction in the relative magnitude of I_{\max} with a concom-

itant increase in the ability to effectively resist bending in the transverse plane.

The variable normally used to assess the resistance of a structure to torsional stress is J , the polar moment of inertia, and is expressed as the sum of the two second moments of area. However, since values of J cannot be extracted from the published data of Daegling and Grine (1991), and more importantly, because polar moments are poor indicators of torsional rigidity in noncircular cross sections (Piziali et al., 1980), the bending index is used here to compare the degree of relative torsional, or bending, rigidity in the *Otavipithecus* mandible with the comparative sample. In general, increased values of I_{\min} , I_{\max} , and J for a given cross section indicate enhanced resistance to bending and twisting of the mandible in response to the stresses incurred during mastication.

It is difficult to directly compare the *Otavipithecus* specimen within the context of the comparative samples' mean values since means for individuals are not directly comparable to means for species. Therefore, in order to evaluate whether cortical and bending indices in *Otavipithecus* are significantly

different from modern apes and fossil hominids at M_1 and M_2 , we used a special case of the single classification analysis of variance (ANOVA), the comparison of a single specimen with a sample (Sokal and Rohlf, 1969).

To test whether the *pattern*, i.e., the difference in the disposition of cortical bone between M_1 and M_2 , in the *Otavipithecus* jaw is unique among living apes and fossil hominids, it is necessary to show that a similar pattern does not occur within the comparative data. Since data on bending index values for individual specimens in the comparative sample are not available in the literature, we have constructed a series of statistical equations based on the assumed covariation between bending index values from M_1 to M_2 (Appendix). Fortunately, cortical index values for each specimen in the hominoid sample are available in the literature (Daegling, 1989) so that it is possible to discern whether any individual in the comparative sample exhibits a similar disparity in cortical index values from M_1 to M_2 .

RESULTS

Cross-sectional geometric properties for each of the eight images are listed in Table 1 along with the range, standard deviation (SD), and coefficient of variation (CV) of each variable. Mean values for both the bending and cortical indices for the comparative sample and *Otavipithecus* and the percentage differences in index values between M_1 and M_2 are presented in Table 2.

Bending index (I_{\min}/I_{\max})

At M_1 . The bending index for *Otavipithecus* at M_1 is lower than the mean value for any species in the comparative sample. It is closest to the mean value of the thick-enamelled extant hominoid, *Pongo*, although it also falls well within the range of *Homo* (Table 2; Fig. 2). *Otavipithecus* falls at the margin of the lowest end of the range for the thin-enamelled *Gorilla* and lies completely outside the range of the other thin-enamelled African ape, *Pan*. In general, the African apes have higher bending indices than *Homo* and *Pongo*; however, these differences are not statistically significant (Daegling and Grine, 1991). *Otavipithecus* also lies sub-

stantially below the ranges of both *A. africanus* and *A. (P.) robustus*.

At M_2 . In sharp contrast to the situation at M_1 , the bending index for *Otavipithecus* at M_2 is higher than the mean value for any of the extant sample (Table 2; Fig. 2). It is closest to the mean value of *Homo*, but falls within the uppermost portion of the ranges of all modern forms except *Pan*. The value for *Otavipithecus* also falls within the ranges of *A. (P.) robustus* and *A. africanus*. Overall, the bending index for *Otavipithecus* lies between the means of extant hominoids and South African hominids.

Results from the single classification ANOVA indicate that at the level of M_1 , *Otavipithecus* is statistically significantly different from *A. (P.) robustus* ($P < .05$). Although *Otavipithecus* falls outside the range of *A. africanus*, they are not significantly different from one another. This may be due to the very large standard deviation and the small number of specimens in the *A. africanus* sample. At the level of M_2 , *Otavipithecus* is significantly different from *Pan*.

The mean value of I_{\min} increases slightly from M_1 to M_2 ($\Delta I_{\min} = 15.5\%$) compared with the large reduction in I_{\max} ($\Delta I_{\max} = -35.6\%$). Thus, the overall caudal increase in the bending index of *Otavipithecus* is driven by I_{\max} .

The results of the statistical tests in the Appendix indicate that for all pairwise comparisons when $r = 1$, the bending index *pattern* in *Otavipithecus* is significantly different ($P < .05$) from early hominids and living hominoids. When $r = 0$ and $r = -1$, none of the pairwise comparisons are significantly different ($P > .05$) (see Appendix).

Cortical index (CBA/TSA)

At M_1 . The value for *Otavipithecus* is closest to the thin-enamelled African apes and *Homo*, and just within the uppermost extent of the *Pongo* range (Table 2; Fig. 2). Thus, *Otavipithecus* does not differ from the condition seen in most hominoids. *Otavipithecus* also fits within the ranges of both fossil hominid taxa; however, it lies at the lower end of the *A. (P.) robustus* range.

TABLE 2. Cross-sectional properties of *Otavipithecus namibiensis*, extant hominoids, and early hominids

	M ₁		M ₂		Percentage difference ¹
	Mean (n)	Range	Mean (n)	Range	
Bending index					
<i>Pan</i>	379.4 (10)	287–495	370.1 (10) ²	277–449	–2.5
<i>Pongo</i>	303.4 (10)	218–412	346.4 (10)	162–536	14.2
<i>Gorilla</i>	361.0 (10)	283–474	386.6 (10)	305–530	7.1
<i>Homo</i>	333.4 (10)	240–425	414.8 (10)	330–578	24.4
<i>Otavipithecus</i>	283.4 (1)		509.3 (1)		79.7
<i>A. (P.) robustus</i>	672.7 (7) ²	594–839	688.3 (6)	474–759	26.3
<i>A. africanus</i>	538.4 (5)	359–681	680.0 (4)	506–816	2.3
Cortical index					
<i>Pan</i>	363.5 (10)	210–438	389.7 (10)	269–488	7.2
<i>Pongo</i>	305.4 (10)	208–360	391.9 (10)	181–407	–4.6
<i>Gorilla</i>	387.9 (10)	281–513	369.0 (10)	259–448	–5.1
<i>Homo</i>	378.2 (10)	293–489	368.8 (10)	324–438	–2.5
<i>Otavipithecus</i>	360.0 (1)		299.0 (1)		–20.4
<i>A. (P.) robustus</i>	391.1 (7)	357–423	352.2 (6)	301–466	–5.4
<i>A. africanus</i>	313.0 (5)	278–410	297.0 (4)	208–400	–11.0

¹Expressed as: [(value for M₂ – value for M₁)/value for M₁] × 100. A negative percentage difference therefore indicates a decrease in the index value from M₁ to M₂.

²Significantly different from *Otavipithecus* at *P* = .05 level.

Adapted from Daegling and Grine, 1991.

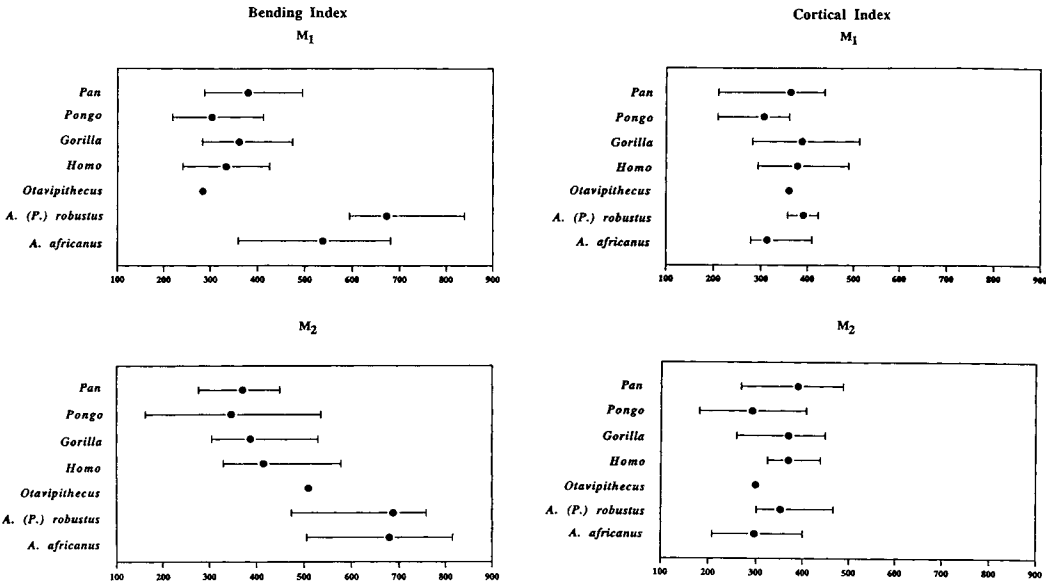


Fig. 2. Comparison of bending (left) and cortical (right) index values of *Otavipithecus* with the comparative sample at the level of M₁ and M₂. Circles indicate species means while horizontal lines indicate ranges.

At M₂, *Otavipithecus* most closely approximates the condition seen in *Pongo* and *A. africanus* and lies below the means of all other modern forms and *A. (P.) robustus* (Table 2; Fig. 2).

Results from the single classification ANOVA indicate that *Otavipithecus* does not

differ significantly from any of the extant or extinct taxa at either M₁ or M₂. As far as cortical index patterns are concerned, for all specimens in the hominoid sample only three (two *Pongo* males and one *Gorilla* female) of 40 individuals exhibit a similar disparity in cortical index values between M₁ and M₂.

The mean value of CBA decreases from M_1 to M_2 ($\Delta CBA = -13\%$) compared with the slight increase in TSA ($\Delta TSA = 4.7\%$). Thus, the caudal decrease in the cortical index value for *Otavipithecus* is driven by CBA.

DISCUSSION

Masticatory stress regimes

In order to provide a context for the interpretation of the cross-sectional geometry of the *Otavipithecus* mandible, a brief overview of the various stress regimes which may play vital roles in the form of the mandibular corpus is necessary. During the power stroke of mastication and unilateral molar biting, the mandible undergoes bending in both the parasagittal and transverse planes, twisting (torsion) about the long axis of the mandible, and shearing in the dorsoventral plane (Hylander, 1979a,b, 1984, 1985, 1988). The ability of the corpus to counteract these masticatory stresses is directly related to certain biomechanical properties. For instance, resistance to bending in the parasagittal plane is directly proportional to I_{max} . Increases in I_{max} can be brought about through the deposition of cortical bone on the superior and inferior borders of the corpus, thereby resulting in a vertically deep mandible (Hylander, 1979a,b). Lateral bending of the corpus in the transverse plane is best counteracted by increasing I_{min} . This is most easily achieved by the deposition of cortical bone along the medial and lateral borders of the corpus (Smith, 1983; Kelley and Pilbeam, 1986), resulting in a thickening of the mandible transversely.

Twisting, or torsional, stresses are greatest along the posterior regions of the corpus due to the oblique orientation of the long axis of the tooth row with that of the mandibular body (Hylander, 1979b). The ability of the corpus to resist torsional stress is directly proportional to the magnitude of the bending index. The areas experiencing the maximum torsional stress are the medial and lateral aspects of the corpus, so that increases in the magnitude of I_{min} relative to I_{max} (i.e., a thickening of the mandible transversely) will maximally counteract torsional stresses (Hylander, 1979a,b).

Cross-sectional geometry of *Otavipithecus*

Bending index. Bending index values remain fairly constant for early hominids and modern hominoids from M_1 to M_2 (ranging from -2.5 to 26.3% difference) (Table 2). Early hominid mandibular corpora at both regions are characterized by a more circular cross section while those of extant hominoids are generally deeper. *Otavipithecus* appears to be unique in that at M_1 the corpus is relatively deeper thereby resembling modern hominoids (i.e., possesses a low bending index) whereas at M_2 , the cross section becomes more circular thereby resembling early hominids (i.e., possesses a higher bending index) (Table 2).

There are at least four possible explanations for this unusual shift in the internal organization of the *Otavipithecus* mandible between M_1 and M_2 : 1) From a biomechanical perspective, the unique mechanical design of the *Otavipithecus* mandible could represent a structural response to heavier transverse bending loads in the posterior molar region. *Otavipithecus* exhibits a lateral bulging of the corpus at the level of M_2 due to the confluence of the corpus with the anterior aspect of the ramus, thereby resulting in an increase in cortical bone thickness with a concomitant increase in the value of I_{min} . Maximizing values of I_{min} will increase the ability of the corpus to counteract transverse bending loads. 2) The increase in relative torsional rigidity posteriorly, brought about by a relative increase in I_{min} , could also represent a structural response to increased torsional loads in the posterior molar region. 3) The posterior mandibular corpus of *Otavipithecus* could have been reorganized to maximally resist an increase in both transverse bending and torsional loads. 4) The arrangement of the ramal root with respect to the corpus, and the concomitant increase in I_{min} , may be an artefact of small mandibular (i.e., body) size, rather than a structural response to increased masticatory stresses.

Given that several scenarios may explain the unique cross-sectional morphology of the *Otavipithecus* mandible, is it possible to discriminate among them? According to Hylander's theoretical model, transverse bend-

ing stresses should be greatest at the symphysis and decrease posteriorly along the mandible (Hylander, 1979b). Thus, higher bending indices (or greater values of I_{\min} relative to I_{\max}) should be associated with more anteriorly located positions along the corpus. In the comparative sample, however, bending indices actually increase from M_1 to M_2 in all taxa except *Pan* (Table 2). Percentage increases in index values range from 7.1% (*Gorilla*) to 24.4% (*Homo*) for modern hominoids and from 2.3% in *A.(P.) robustus* to 26.3% in *A. africanus*. In *Otaviopithecus*, however, the percentage increase in bending index is 79.7%, over three times as great as the maximum increase within the entire comparative sample. Thus, it is unlikely that the biomechanical shape of the *Otaviopithecus* posterior corpus can be explained solely as a response to an increase in transverse bending loads.

One possible effect of an increase in I_{\min} is an increase in J , the variable normally used to assess resistance to torsional loads. However, polar moments are only reliable indicators of torsional rigidity in circular sections. For example, in the case of *Otaviopithecus*, where the shape of the cross section is highly elliptical, J actually decreases (from 8038.8 mm⁴ to 6074 mm⁴, or $\Delta J = -24.5\%$) as I_{\min} increases.

The most effective way to maximally enhance resistance to torsion, i.e., increase relative bending rigidity, is through the deposition of cortical bone on the medial and lateral aspects of the corpus, thereby increasing the magnitude of I_{\min} relative to I_{\max} and thus raising the value of the bending index. Hylander's model suggests that due to the orientation of the tooth row with the corpus, measures of torsional rigidity should increase posteriorly. Thus, bending index values should increase from M_1 to M_2 . This prediction is borne out by the data presented in Table 2 which show such an increase in bending index values for almost all taxa (except *Pan*) in the comparative sample. Given that the increase in the bending index of *Otaviopithecus* is driven by an increase in I_{\min} relative to I_{\max} , the differential arrangement of compact bone is more likely a response to increased torsion brought about by an increase in transverse bending loads.

The last explanation maintains that the increase in bending index values for *Otaviopithecus* is an artefact of its small body size and more compact mandible. Thus, the increase in torsional rigidity would be a result of the relative positioning of the ramal root with respect to the tooth row and would not represent a structural response to increased masticatory loading. *Otaviopithecus* has an estimated body mass of approximately 14–20 kg (Conroy et al., 1992), a much smaller body size than any of the taxa in the comparative sample. Therefore, a more valid comparison would be with the small-bodied hominoid, *Hylobates lar* (5.3–5.7 kg).

As in all comparative studies, it is necessary to control for differences in shape which may be attributable to differences in overall size. Therefore, it is important to determine whether the unusually high bending index value at M_2 in *Otaviopithecus* is an allometric effect of small body size. The most appropriate method to test this hypothesis is to relate second moments of area to total mandibular length, the mechanically relevant variable necessary to determine mandibular robustness (Daegling, 1990). Given the fragmentary nature of the *Otaviopithecus* specimen, however, it is impossible to reconstruct this variable with any degree of accuracy. An alternate method, therefore, is to compare scaled bending indices of *Otaviopithecus* and *H. lar* with that of the larger-bodied extant hominoids.

Bending index values for *H. lar* are 282.4 (M_1) and 362.7 (M_2) (Daegling, 1990); $\Delta BI = 80.3$ or an increase of 28.4%. At M_1 , the bending index is nearly coincident with that of *Otaviopithecus* while it is much lower at M_2 . The percentage increase in *Hylobates* is greater than that seen in all other extant hominoids and fossil hominids but far less than in *Otaviopithecus*.

The hypothesis that the unique arrangement of *Otaviopithecus*' posterior corpus is an artefact of small mandibular, and thus, small body size, was tested by analyzing bending index values at M_2 relative to body size (Fig. 3). Despite similarities in body size and orthognathism relative to other hominoids, *Otaviopithecus* and *Hylobates* are structurally dissimilar in the design of the posterior corpus. *Otaviopithecus* lies far

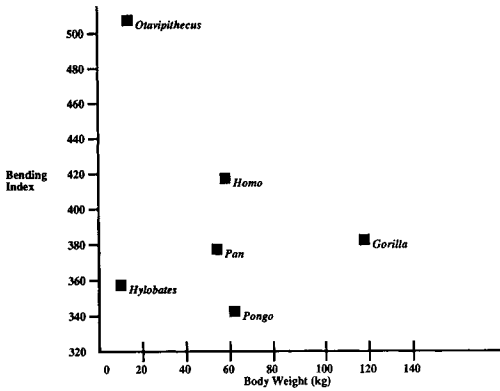


Fig. 3. Bivariate plot of bending index values (relative bending rigidity) of the mandibular corpus at M_2 relative to body mass in extant apes, humans, and *Otavipithecus*. Each point represents a species mean. Note the position of *Otavipithecus* and *Hylobates* relative to the cluster of extant large-bodied hominoids and to one another. Bending index data for extant hominoids from Daegling (1990), all body weight data from Fleagle (1988).

above the cluster of extant hominoids indicating that it possesses a much higher bending index at M_2 than expected for a hominoid of its body size. Thus, the increase in relative torsional rigidity in *Otavipithecus* is most likely a structural response to increased masticatory loads rather than a morphological artefact of a smaller, more compact mandible.

Cortical index. Regardless of bending index values, cortical indices for hominids and hominoids are fairly homogeneous. *Pongo* and *A. africanus* do possess lower indices than the remainder of the modern hominoid and hominid sample. Given that torsional forces were high in early South African hominid taxa, the low cortical index in *A. africanus* indicates a more economical use of material than its robust counterpart to achieve a similar mechanical design. Thus, *A. africanus* "achieved [a similar degree of] torsional rigidity with relatively less cortical area" (Daegling and Grine, 1991: 328).

At both regions of the corpus, *Otavipithecus* falls well within the ranges of modern hominoids and early hominids. It differs, however, in that cortical index values decrease sharply towards the posterior corpus

(Table 2). Therefore, as in *A. africanus*, the *Otavipithecus* mandible achieves a relatively high degree of torsional rigidity (as evidenced by the high bending index) at M_2 with a minimum investment of cortical bone. In other words, *Otavipithecus* exhibits a highly economic utilization of compact bone in the posterior corpus in order to dissipate torsional and transverse bending loads similar in magnitude to those experienced by both species of South African hominids.

There is usually a high correlation between molar enamel thickness, corpus dimensions, and certain biomechanical variables (Smith, 1983). Thicker enamel is most likely an adaptation to help dissipate the forces associated with mastication. Taxa with increased masticatory loadings should exhibit higher bending index values. One might therefore expect a tight correlation between the thickness of the enamel over the molars and the structural design of the mandibular corpus, i.e., taxa whose mandibles are subjected to increased loading should exhibit relatively thicker enamel. In fact, *A. (P.) robustus*, and to a lesser extent *A. africanus*, which exhibit the highest degrees of torsional rigidity, and presumably torsional stresses, are also characterized by the thickest enamel. The results of our analysis on *Otavipithecus* seem to contradict this hypothesis. *Otavipithecus* has thinner enamel than most Miocene hominoids (Conroy et al., 1992, 1995) and yet is more similar to the thick-enamelled hominoids and early hominids for several biomechanical and geometric properties.

CONCLUSION

It is generally accepted that early hominid mandibles were adapted to resist relatively high twisting moments in the posterior molar region, whereas modern hominoids are not. Based on the data presented here, it seems clear that torsional stresses were acute in the posterior corpus of *Otavipithecus*. The internal organization of the mandible allowed it to effectively resist these increased loads by means of a highly efficient mechanical design, i.e., the economic deployment of compact bone to achieve a relatively high degree of torsional rigidity. Similar me-

chanical design is seen only in *Pongo* (although torsional stresses in the posterior corpus of that taxa are not nearly as great) and *A. africanus*. While torsion may or may not have been the major source of stress, it seems to have assumed a more critical role in *Otaviipithecus* than in any modern hominoid. An examination of the geometric design of other Miocene hominoid mandibles should shed more light on whether the constellation of biomechanical and morphological attributes seen in *Otaviipithecus* is truly unique among fossil apes.

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APPENDIX

The basis for the equations is the following: $v_{m2-m1} = v_{m1} + v_{m2} - 2\text{cov}_{m1m2}$, where v is the variance and cov is the covariance. For $r_{m1m2} = -1$, the $\text{cov}_{m1m2} = -\sqrt{v_1 - v_2}$ where r is the correlation. Since v equals the standard deviation squared, the equation can be rewritten as: $s_{m2-m1}^2 = s_{m2}^2 + s_{m1}^2 + 2(s_{m2}s_{m1})$ where s is the standard deviation. Thus, low bending index values at M_1 correspond to

relatively high values at M_2 and vice versa. If $r = 0$, i.e., no correlation between bending index values at M_1 and M_2 , then $s_{m2-m1}^2 = s_{m2}^2 + s_{m1}^2$. For $r = 1$, $s_{m2-m1}^2 = s_{m1}^2 - 2(s_{m2}s_{m1})$, where low bending index values at M_1 correspond to relatively low values at M_2 and vice versa. The resultant s_{m2-m1}^2 value was then submitted to a single classification ANOVA. The test was run for each taxon versus *Otavipithecus* under the null hypothesis that both samples are from the same statistical population, i.e., there is no difference between the pattern in both taxa under comparison. So, for example, according to the first model (where $r = -1$), the equation tests the hypothesis that the bending index pattern in *Otavipithecus* is not unique but rather expected.